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Life history of *Stegodyphus dufouri* (Audouin, 1825) (Arachnida: Araneida: Eresidae) in Egypt, A step on the way from asocial to social

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Abstract

Stegodyphus dufouri (Audouin, 1825) was reared under laboratory conditions to study its life history. Males reached maturity after 6-7 instars (116.5 ± 8.746 days), and females after 7 instars (124.36 ± 6.404 days). Adult longevity of male: 48-311 days, and female 99-441 days. Life span of male: 165-437 days, and female 224-569 days. Some spiderlings were reared together (communal rearing). The second generation was also kept together for more observation. Different kinds of prey were used for feeding different instars of spiderlings. Behavioural observations were reported on this spider both in nature and laboratory. These observations lead to a conclusion that the behaviour of this species is a step on the way to social life.

Keywords: Life history, Spiders, Eresidae, *Stegodyphus dufouri*, Egypt, Sociality.

Introduction

Family Eresidae C. L. Koch, 1851 includes 95 species and 7 subspecies, from Africa, Asia, Europe and Brazil, classified within 10 genera (Platnick, 2003). Genus *Stegodyphus* Simon, 1873 is the second big genus, in number of species, of family Eresidae. It includes 21 species from Africa, Asia, southern Europe and Brazil (Platnick, 2003). *Stegodyphus* species build their nests on plants or buildings. Some of them are solitary (i.e. every individual lives alone in a separate nest), and others are social (i.e. live in colonies). Kraus & Kraus (1988) defined three species groups of *Stegodyphus* species: *africanus*, *dufouri* and *mirandus*. Each species group includes both solitary and social species. The first *Stegodyphus* species was discovered in

Egypt and described under the name *Eresus Dufourii* in "*Description de l'Égypte*", plate 4, fig. 12, of Napoleon's expedition to Egypt (Audouin, 1825; El-Hennawy, 2000). *Stegodyphus dufouri* (Audouin, 1825) is recorded from North, East and West Africa and Yemen (Kraus & Kraus, 1988). In Egypt, *S. dufouri* (Fig.1) is widely distributed in the Nile Valley and is found in the Western Desert and Sinai (El-Hennawy, 1987b, 1990, 1992, 2002a).

El-Hennawy (1985, 1986, 1987a) studied the relation between *S. dufouri* and the pompilid wasp *Pseudopompilus humboldti* (Dahlbom, 1845). He reported that females of *P. humboldti* attack and paralyse adult females of *S. dufouri* and that their larvae devour the paralysed spiders to complete their metamorphosis to the adult stage (i.e. wasps). This relation was almost the only available information on the biology of *S. dufouri* (Kraus & Kraus, 1988; Seibt & Wickler, 1988a). In 1986, El-Hennawy also reported few notes on the biology of *S. dufouri*. And recently, he summarized the relationship between the mother and her brood (El-Hennawy, 2002b). The life cycle of this spider was not yet studied. Therefore, we decided to rear *S. dufouri* in laboratory to study some aspects in its life cycle. We reported too some observations on this spider both in nature and laboratory.

Fig. 1. *Stegodyphus dufouri* (Audouin, 1825), male and female.

Material and Methods

Adult individuals of *Stegodyphus dufouri* (Audouin, 1825) were collected from Siwa Oasis, in the Western desert of Egypt, by the first author (HE): 6 ♂, 10 ♀ 18 May 2001, Siwa Oasis, nests on wild and cultivated plants in a field, 29°12'11"N 25°30'49"E; 1 ♂, 1 ♀ 20 May 2001, Siwa Oasis, inside a common nest on a plant beside Amun Temple, 29°12'21"N 25°32'55"E.

All spiders were reared under laboratory conditions, 26-28^{o}C and 60-70% R.H. in the laboratory of the second author (MM) in Faculty of Agriculture, Al-Azhar University. Every adult specimen was individually reared inside a glass cylinder (13 cm diameter, 25 cm height), including in its middle a bar of wood (1x5x22 cm). Each glass cylinder was located over a plastic pot (20 cm height, 15 cm diameter) filled with sand to fix the glass cylinder. Some spiderlings, produced in the laboratory, were reared individually (31 spiderlings) after 1st moulting and some of them together (39 spiderlings; communal rearing). The second generation was kept together for more observation. Different kinds of prey were used for feeding different instars of spiderlings (see food consumption section).

Results

Parents – Eggs – Spiderlings

The male and female of *S. dufouri*, found together inside a nest on a plant beside Amun Temple in Siwa Oasis (20 May 2001), were reared together to mate in laboratory (1 June 2001). After 10 days (Preoviposition period), the female laid eggs in a light yellow slightly swollen circular egg-sac (its diameter = about 10 mm). The mother kept the egg-sac among her first and second pairs of legs and under her body. The eggs hatched on 5 July (Egg incubation period = 24 days) yielding 70 spiderlings. The mother died on 9 July after feeding the spiderlings on her body, which they suck dry. [Feeding by regurgitation was not evidently observed.] We reared 31 of the spiderlings individually, after 1st moulting, in separate glass vials and 39 spiderlings together (communal rearing).

During rearing individual spiderlings, 7 individuals died before reaching maturity (Mortality before maturity: 22.58%): 1 died after 2nd moulting, 3 died after 3rd moulting, 2 died after 4th moulting, and 1 died after 5th moulting. Those individuals were excluded from the calculation of instars' duration. The remaining 24 individuals reached maturity; 10 males (41.67%) and 14 females (58.33%). [Sex ratio, ♂/♀ = 0.7] All females reached maturity after 7 moults while 6 males (60%) reached maturity after 6 moults (6 instars) and 4 males (40%) moulted 7 times (7 instars). The duration of every instar is shown in Table 1. The life cycle duration, 1-6/7 instars, was 107-133 days for males and 109-131 for females.

Table 1: Duration of different stages of *Stegodyphus dufouri* (Audouin, 1825).

Developmental stage	Duration (days)					
	Male			Female		
	Range	Mean	S.D.	Range	Mean	S.D.
1st instar	24-27	25.4	1.430	24-28	25.29	1.383
2nd instar	25-29	27.3	1.252	25-29	27.64	1.151
3rd instar	12-15	13.2	1.033	10-14	13.21	1.122
4th instar	17-20	18.8	1.033	17-21	18.64	1.336
5th instar	11-17	14.8	1.874	12-16	14.36	1.151
6th instar	7-19	11.3	4.900	7-19	10.64	3.934
7th instar *	13-16	14.25	1.5	6-20	16.00	3.843
Life cycle	107-133	116.5	8.746	109-131	124.36	6.404
Adult longevity	48-311	120.5	77.479	99-441	233.86	117.870
A.l. **	48-110	80.43	20.024	99-172	142	30.298
Life span	165-437	237	82.857	224-569	358.07	115.398

* = only 4 individuals of 10 males; all females.
** = Adult longevity of 7 individuals which lived 48-110 days (♂) and 99-172 days (♀).
Note. Egg incubation period is not included neither in "Life cycle" nor in "Life span".

Adults – Life span

The spiderlings became adult males 107-133 days after hatching from eggs, and died after longevity of 48-311 days. Males began to die in December 2001 until February 2002. Two males lived until April 2002 and only one lived until September 2002, i.e. exceeded one year life span!. The spiderlings became adult females 109-131 days after hatching from eggs, and died after longevity of 99-441 days, much longer than males. Females began to die in February until July 2002. Three females lived

until November 2002 and only one lived until January 2003. Five females exceeded one year life span, one of them exceeded 18 months. The variation of life span of both males and females appears evidently in Fig. 2.

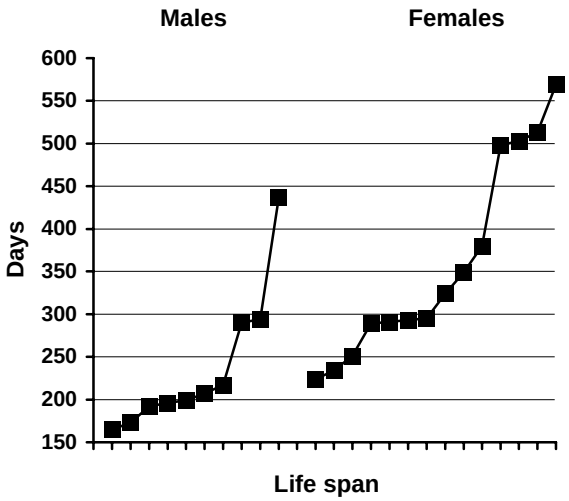


Fig. 2. Life span of adult males and females *Stegodyphus dufouri* reared in laboratory.
(300 days: 1 May 2002)

Food consumption

Four different preys were used in feeding spiderlings and adults of *S. dufouri*. Two larvae of Lepidoptera: Cotton leaf worm (moth) *Spodoptera littoralis* (Boisduval, 1833) and Lesser wax moth *Achroia grisella* (Fabricius, 1794), and two flies of Diptera: Fruit fly *Ceratitis capitata* (Wiedemann, 1824) and House fly *Musca domestica* Linnaeus, 1758.

Feeding rate (every two days): 1st instar spiderlings were fed together on 15 larvae of 1st – 3rd instars of *A. grisella*; every 2nd instar spiderling was fed on one 2nd instar larva of *S. littoralis*; every 3rd instar spiderling was fed on one 3rd instar larva of *S. littoralis*; every spiderling or subadult spider of 4th – 7th instars was fed on a mixture of *C. capitata* and *M. domestica*; adults were fed on the same mixture with the increase of the quantity according to the spider's size. Number of consumed preys by different spiderling instars is in Table 2.

Table 2: Food consumption of *Stegodyphus dufouri* (Audouin, 1825) in laboratory.

Developmental stage	Prey	Male			Female		
		Range	Mean	S.D.	Range	Mean	S.D.
1st instar	*Achroia grisella*	5.76-6.48	6.10	0.343	5.76-6.72	6.07	0.332
2nd instar	*Spodoptera littoralis*	12.5-14.5	13.65	0.626	12.5-14.5	13.82	0.575
3rd instar		6-7.5	6.6	0.516	5-7	6.61	0.561
4th instar	*Ceratitis capitata* & *Musca domestica*	17-27	20.6	3.502	18-31.5	26.57	3.502
5th instar		16.5-28	22.9	3.307	22.5-35	28.14	3.692
6th instar		14-38	21.75	9.041	17.5-51	29.07	10.301
7th instar *		30-64	46.25	14.886	30-85	67.43	14.155

* = only 4 individuals of 10 males; all females.

Egg-sacs

The females which reached maturity in laboratory were admitted to mate with adult males and they constructed 7 egg-sacs in July, August and September 2002. The egg-sacs were light yellow coloured and circular in shape. The diameter of the smallest egg-sac was 8 mm, and the largest was 12 mm (10.25 ± 1.332).

Individually reared spiders: A female had an egg-sac (10 mm, 199 eggs) which did not hatch, then she constructed another one (10.5 mm, 55 eggs) which did not hatch too. Another female constructed two egg-sacs (8 mm, 193 eggs in August and 12 mm, 257 eggs in September) which did not hatch.

Communally reared spiders: One female, which mated when she was among the group, laid 64 eggs in 2.8.2002 (45 hatched in 11.9.2002 and 19 did not hatch). The same female laid eggs again in 21.8.2002 (11 mm, 231 eggs); 12 of the eggs hatched and died inside the sac. Another unhatched egg-sac (10 mm, 200 eggs) was found in the communal rearing container without definite mother.

Observations

A. In Laboratory – Communal rearing

The 39 spiderlings which were reared together (i.e. communally) until reaching maturity did not feed on each other (no cannibalism). There was a competition on preys among spiderlings, hence there was a great variation in their sizes and a few reached maturity while the majority of them were still juvenile. Generally, communal reared spiderlings had smaller body size in comparison with individually reared counterparts. Cooperation to subdue prey by spiderlings and living on a common web were noticed.

The only fertile egg-sac was laid by a female mated when she was living among others, i.e. communally. Her brood (45 spiderlings) was reared together too. No regurgitation was noticed. The spiderlings did not feed on their mother's body. The first spider reached maturity, among this 2nd generation, was a male in 25.1.2003 while the other individuals were still young and smaller in size. The mother lived and laid eggs again.

B. In Nature

Most of the following observations were reported in 1978-1980 in Cairo and several localities in the Nile valley and some of them were published by the first author (El-Hennawy, 1986).

Mother and brood

1. The female *S. dufouri* always has one egg-sac. She keeps it under her cephalothorax and among her anterior legs. She leaves it to attack prey at the entrance of her nest. She comes back fast to protect it if there is a stronger attacker. If she is disturbed by a slim stick she bites it.
2. The spiderlings, amber coloured, cannot emerge from the egg-sac without their mother's aid. She opens the sac using her fangs.
3. If the mother does not open the egg-sac (because of predation or parasitism) the spiderlings do not emerge and die inside the sac. And even if the spiderlings could leave the sac (I opened several sacs), they cannot move easily with their rounded, soft abdomens and cannot attack prey.
4. The mother feeds her offspring by regurgitation.
5. If an enemy, a predator or even a human finger, attacks the nest trying to enter, the mother defends in a fast vigorous rush against it and bites the enemy.
6. After a few days, the mother closes the nest's entrance with silk, turning it to a closed chamber. The mother's body becomes "digested-like". Then the spiderlings (1-1.5 mm) begin to feed on their mother's body, which they suck dry.

Nest

7. After moulting, the spiderlings change the design of the mother's nest, which is a chamber of silk with one entrance (1.5-2 cm) inside a fluffy mass of silk threads (about 5x8 cm), to a group of attached retreats among two layers of silk around the main old chamber. The retreats have small entrances on the surface of the nest (Figs. 5-7). The silk web attached to the nest is neglected by the spiderlings which do not

depend on it in getting food. Later, they construct a new web attached to the nest and around it.
8. After more moults, the spiderlings find their way to the outside world. Everyone constructs its own nest. Most small nests are near ground surface. A few nests temporarily contain more than one individual.
9. The nests of adults which are on plants or on buildings maybe too near to each other but never attached. Adults prefer higher places on plants for nests which are mostly in the way of wind and exposed to sun. Entrance of the nest is mostly downwards.

Prey and predation
10. Feeding in nature is mostly on Diptera, but also Hymenoptera (specially wasps and ants), few Coleoptera, Lepidoptera and Neuroptera, and other insects are reported. (Carcasses of different preys are found stuck to the nest's silk.)
11. Two strong preys are recorded: a. Oriental Hornet, *Vespa orientalis* Linnaeus, 1758 [Hymenoptera, Vespidae] and b. Mole Cricket, *Gryllotalpa gryllotalpa* Linnaeus, 1758 [Orthoptera, Gryllotalpidae]. The first predates spiders while the second is more than twice the size of the adult female *S. dufouri*. The spider depends on venom and stickiness of silk to subdue prey.
12. The spiderlings cooperate in subduing prey. They attack prey which lands or moves on their nest's wall. They come out of their retreats to catch legs and wings of the prey simultaneously. Sometimes, one spiderling begins the attack and the others follow him. Their attack is similar to that of a group of wolves.

Natal philopatry
13. The spiderlings do not leave their nest when somebody destructs a large part of it. They stay inside it, despite they cannot repair it. Only great disturbance can push them out of it.
14. In an old experiment (15.1.1979), five spiderlings, separated from their mother's nest, were kept in a large container distant from each other. They aggregated and made a small common nest.

Discussion

This is the first study of the life history of the African eresid *Stegodyphus dufouri*. This species belongs to the *dufouri* group, one of the three species groups of *Stegodyphus* species: *africanus*, *dufouri* and *mirandus*. Each species group includes both solitary and social species (Kraus & Kraus, 1988). Only, the life history of the social species, of the *dufouri* group, *Stegodyphus sarasinorum* Karsch, 1891, was studied by Jacson & Joseph (1973). "Unfortunately, up to now the biology of the social species' solitary sister species is practically unknown." (Seibt, *et al.*, 1998).

Life history

Ten days after mating in laboratory (Preoviposition period), the female built an egg-sac and laid eggs. Eggs hatched after 24 days (Incubation period), and 70 spiderlings emerged out of the cocoon. Kullmann *et al.* (1972) stated that the eggs of *S. pacificus* Pocock, 1900, a solitary species of the *dufouri* group, from Afghanistan, need 24-38 days in laboratory to hatch. They determined the number of eggs per cocoon as: 259-608. *S. pacificus* is very similar to *S. dufouri*. "It is practically impossible to distinguish the two forms by their genitalic characters…It is therefore possible – perhaps even probable – that the two allopatric forms of *dufouri* … and the

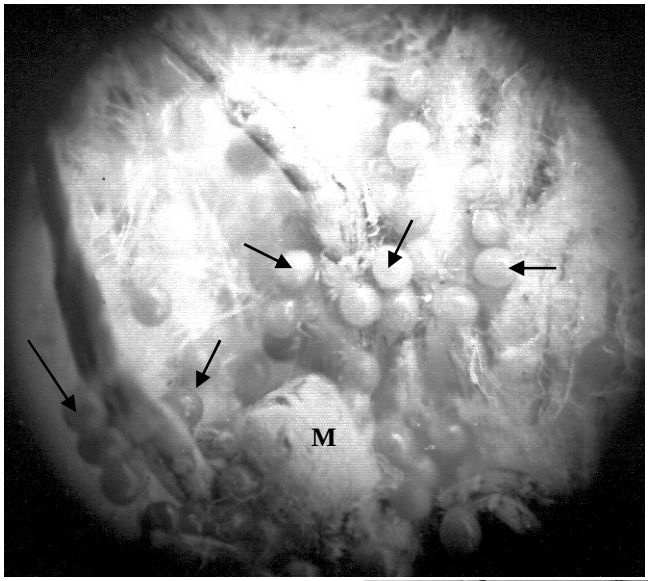
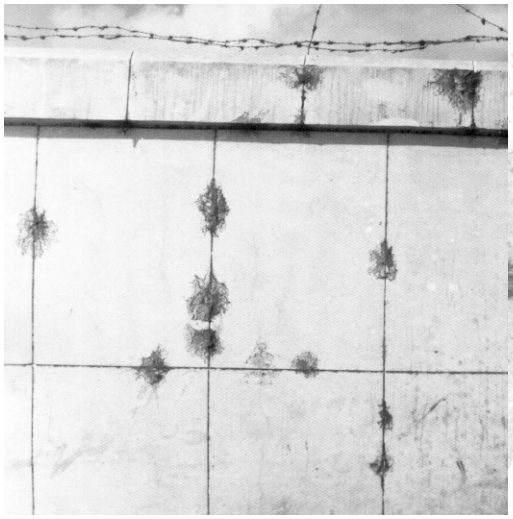
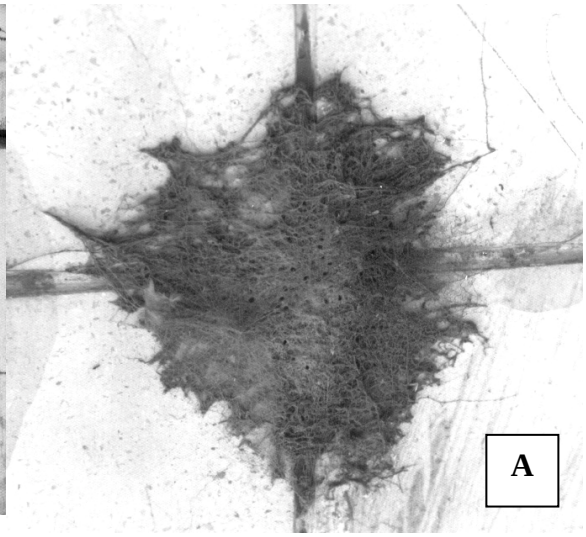


Fig. 3. Spiderlings of *Stegodyphus dufouri*, 1st instar, feeding on their mother's body inside their nest. (M = mother's cephalothorax; arrows = some spiderlings)

Fig. 4. Aggregated nests of *Stegodyphus dufouri* on a store of cereals, in Beni Suef town.





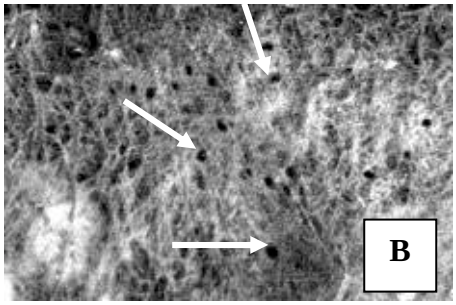


Fig. 5. Nests of *Stegodyphus dufouri* on a wall, in Zagazig town. A. One of the nests, with several entrances. B. Some entrances (arrows).

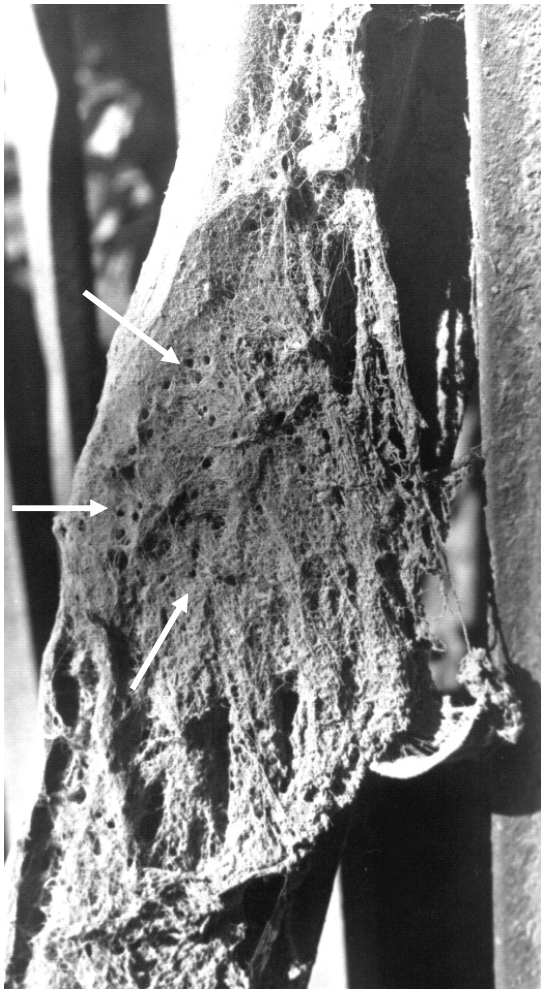


Fig. 6. A communal nest of the spiderlings of *Stegodyphus dufouri* on the fence of the train station in Assiut town with several entrances. (arrows = some entrances)

Fig. 7. Another communal nest of the spiderlings of *Stegodyphus dufouri* on plants in Kom Osheem, El-Fayum. (arrows = some entrances)

Indian *pacificus*…are merely subspecies of a single, widely distributed polytypic species"(Kraus & Kraus, 1990). Bradoo (1973) recorded 60-115 eggs in the cocoon of *S. sarasinorum*, and 150-250 eggs for *S. lineatus* (Latreille, 1817), of *mirandus* group (after Millot & Bourgin, 1942), while Jacson & Joseph (1973) recorded 110-120 eggs in the cocoon of *S. sarasinorum* that need 21-22 days as incubation period. Seibt & Wickler (1988b) recorded 15-48 eggs per cocoon of the social spider *S. mimosarum* Pavesi, 1883 (*africanus* group). Solitary species usually lay eggs more than social species do.

The adult females of the first generation of *S. dufouri* developed in laboratory laid eggs in 7 egg-sacs. Individually reared spiders laid: 55, 193, 199, 257 eggs in 4 egg-sacs, which did not hatch. Communally reared spiders constructed 3 egg-sacs: a- 64 eggs, 45 hatched and 19 did not hatch, b- 231 eggs, 12 of the eggs hatched and died inside the sac, c- 200 unhatched eggs. It is evident that there is a great variation in number of eggs per egg-sac. This may depend on feeding.

The mother always feeds her offspring, 1st instar, by regurgitation (Several observations in nature, HE), despite this was not evidently observed in laboratory (MM). This behaviour was previously recorded by different authors and photographed too by Kullmann *et al.* (1972, Figs. 11: *S. pacificus*; 15, 16: *S. sarasinorum*). Secondly, the spiderlings fed on the mother's body, which they suck dry, i.e. "gerontophagy" (Fig. 3). The mother died 4 days after the emergence of the spiderlings out of the cocoon. Gerontophagy was also recorded by different authors and photographed by Kullmann *et al.* (1972, Fig. 22: *S. lineatus*) and Jacson & Joseph (1973, Fig. 7: *S. sarasinorum*). Kullmann *et al.* (1972) stated that *S. pacificus* female mostly dies 3-8 days after the emergence of her spiderlings out of the cocoon. *S. dufouri* is a semelparous spider which has extreme maternal care like *S. lineatus* which "normally die after producing a single clutch, while the young are still in the nest"(Schneider & Lubin, 1997).

S. dufouri spiderlings developed, in laboratory, through 6-7 instars before reaching maturity. Kraus & Kraus (1990) recorded that "Females of *S. bicolor* (O. Pickard-Cambridge, 1869), a solitary species of the *dufouri* group, need at least II+10 moultings to acquire sexual maturity.", while Jacson & Joseph (1973) recorded 12 instars for the social species *S. sarasinorum*, of the *dufouri* group too. Kullmann *et al.* (1972) reported that males of *S. lineatus* reach maturity after 7, 8 or 9 moults, and females after 9 moults or later.

During this study, one egg-sac yielded 10 males and 14 females; Sex ratio, ♂/♀ = 0.71. Jacson & Joseph (1973) stated that the sex ratio of *S. sarasinorum* was 0.15-0.28, while Seibt & Wickler (1988a) reported that it was recorded in three references by different authors as 0.14, 0.29, and 0.38-0.45. They also recorded that the sex ratio of two social spiders of the two other species groups were: *S. dumicola* Pocock, 1898 (*mirandus* group) 0.114, and *S. mimosarum* (*africanus* group) 0.108.

The duration of life cycle was nearly the same for both males and females, but the adult longevity was different and usually shorter in males than females (Table 1). Therefore, the difference between the life span of males and females was great (Fig. 2). Most males died through December-February and only one exceeded a whole year life span. Most females died through February-July and five females exceeded one year life span, one of them exceeded 18 months.

"Most spiders are not particular about the type of prey they feed on. Such spiders are called *polyphagous*, that is, they are generalists with respect to their prey."(Foelix, 1996). Although feeding in nature was mostly on Diptera, larvae of two species of Lepidoptera were successfully used in feeding spiderlings (1st – 3rd instars)

in laboratory (MM). The fruit fly and the housefly were used for feeding 4^{th} – 7^{th} instars and adults. They are among the preys of this species in nature. Spiderlings cooperation in subduing prey was observed in nature and laboratory. This "collective" feeding was recorded by different authors and photographed too by Kullmann *et al.* (1972, Fig. 20: *S. sarasinorum*).

Sociality

According to Shear (1970) and Kullmann (1972), *S. dufouri* should be classified as "sub-social" or "periodic-social" species. Kraus & Kraus (1988) described solitary living species as "non-permanenly social". The three main characteristics of sociality, i.e. Tolerance, Interattraction and Cooperation (Kullmann, 1972), were recognized in the behaviour of *S. dufouri*.

No cannibalism was observed among spiderlings. They lived together, aggregated in their mother's nest, i.e. tolerance. They did not leave their nest after the death of the mother, i.e. Natal philopatry. They preferred to stay together, i.e. interattraction (See: Observations, B-13, 14).

Kullmann (1972) stated that cooperation includes: 1- construction of retreats, 2- construction of sheets for capturing prey, 3- capture of prey, 4- communal feeding, 5- individual brood-care, 6- collective brood-care. In the case of *S. dufouri*, maternal brood care was observed (feeding by regurgitation and gerontophagy, i.e. feeding on the mother's body; in addition to guarding the egg-sac and opening it after eggs' hatching). Cooperation of spiderlings (in catching prey, communal feeding and construction of retreats and snares) was also observed. Collective brood-care was not observed. It is one of the collective activities of adults of social species (Kullmann, 1972).

Aggregated nests were observed in nature. The nests of adults were found near to each other but never attached (Figs. 4, 5). This aggregation is surely beneficial. "Aggregations of *S. lineatus* in separate webs appeared to be safer from wasps than were widely dispersed individuals."(Henschel *et al.*, 1996). Aggregated nests maybe better than a colony of adult spiders.

Obligation – Change of behaviour

Kullmann (1972) stated that "Feeding by regurgitation has been found as an obligatory phase of brood-care in … *Stegodyphus*" spp. He also described feeding on mother's body as another "obligatory phase of brood-care". Obligatory phase can be explained as "a command in a program, built in the ROM of the spider" in computer expressions.

As a result of communal rearing, The spiderlings, of a mother of the first generation developed in laboratory, did not feed on their mother's body, i.e. no gerontophagy?. The mother lived and laid eggs again. This maybe due to unnatural conditions. Anyhow, one case is not enough to get a conclusion. In a study on the maternal care in *Gandanameno echinatus* (Eresidae), Kürpick (2000) stated that "Laboratory investigations showed that females of *G. echinatus* take no care of the young. … The young left the maternal tube 3 days after hatching and dispersed after a gregarious period of 3-5 weeks. If the spiderlings were prevented from dispersing after hatching the behaviour of the mother changed: Females offered prey to the young for about 6 months, but no regurgitation or gerontophagy took place." Maternal care is obviously very sensitive to the surrounding conditions. It may increase or decrease according to outer stimulants.

Keeping juveniles of *S. dufouri* together in the same place until reaching maturity may affect their behaviour. Adults mated inside a communal rearing

container, with high tolerance among individuals, and without cannibalism. “The origin of permanently social species in *Stegodyphus* seems to lie in a conversion from communities of juveniles to communities of pedogenetic adults.”(Kraus & Kraus, 1990). It is evident that sub-social behaviour in *Stegodyphus* spiders, like *S. dufouri*, may represent an intermediate step towards sociality.

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